# TINY PLAGIAULACOID MULTITUBERCULATE MAMMALS FROM THE PURBECK LIMESTONE FORMATION OF DORSET, ENGLAND

*by* Z. KIELAN-JAWOROWSKA *and* P. C. ENSOM

ABSTRACT. *Albionbaatar* gen. nov., assigned to the Albionbaataridae fam. nov., in the Plagiaulacoidea, is described upon the basis of *A. denisae* sp. nov. based on minute (about 1·5 mm long) upper premolars (P5) and three anterior upper premolars (0·5–0·9 mm long), all from the Purbeck Limestone Formation of southern England. Two incomplete lower premolars (p4), each found in a sample yielding an upper premolar of *Albionbaatar*, are described as Plagiaulacoidea, fam., gen. et sp. indet., and we speculate whether they may be counterparts of *Albionbaatar*. *Albionbaatar* differs from known multituberculates in having upper premolars with greater numbers of very small cusps, arranged in three longitudinal rows, and P5 with extensive lingual slope covered by transverse ridges. The oblique lingual slope on P5, characteristic of *Albionbaatar*, occurs in previously known plagiaulacoids, where there are no ridges. The structure of *Albionbaatar* shows that the correlation between tooth size and number of cusps characteristic for the Cimolodonta (at least for the Taeniolabidoidea) may not hold for all the Plagiaulacoidea.

SINCE 1986, one of us (P. C. E.) has been washing and screening vertebrate-rich clay deposits of the Purbeck Limestone Formation, principally from Sunnydown Farm Quarry near Langton Matravers, Swanage, Dorset, southern England. The residues have yielded fish, amphibians, reptiles and mammals (Ensom 1987, 1988; Ensom *et al.* 1991). The mammalian collection contains members of the Triconodonta, Docodonta, Symmetrodonta, Peramura and Multituberculata. Previously we described the collection of multituberculate teeth recovered from this site prior to 1988 (Kielan-Jaworowska and Ensom 1992). We showed that the multituberculates from the Purbeck Limestone Formation contain, in addition to the Plagiaulacoidea, members of the Paulchoffatoidea, hitherto unrecorded in the Purbeck Limestone Formation. That material allowed us to propose a new subordinal classification of Late Jurassic and Early Cretaceous multi-tuberculates (Kielan-Jaworowska and Ensom 1991, 1992), and furnished new data on enamel microstructure in plagiaulacoid multituberculates (Fosse *et al.* 1991).

In our earlier paper on Purbeck multituberculates from the Purbeck Limestone Formation of Dorset (Kielan-Jaworowska and Ensom 1992) we omitted reference to one complete upper premolar (DORCM GS 23) and one fragmentary lower premolar (DORCM GS 22), the affinities of which were in contention. Now we feel sufficiently confident of their multituberculate identity to include them in this paper. Additional multituberculate specimens have been recovered from the residues. This new material contains four, possibly conspecific, upper teeth similar to DORCM GS 23, and identified by us as the upper premolars, and a fragmentary lower premolar which was found in a sample yielding an upper premolar. The upper premolars differ from those occurring in the known multituberculates and we assign them to *Albionbaatar denisae* gen. et sp. nov., which we place in the family Albionbaataridae nov., in Plagiaulacoidea.

For the terminology of the teeth described, localities and sampling methods, see Kielan-Jaworowska and Ensom (1992). The seven teeth described in this paper derive from five samples (Nos: 40 – 14·1 kg; 70 – 26·5 kg; 77 – 29·2 kg; 78 – 34·0 kg; 95 – 38·0 kg), all collected from the Cherty Freshwater Member, Purbeck Limestone Formation, near Langton Matravers, Purbeck, Dorset.

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We employ the following abbreviations: BMNH – Natural History Museum (previously British Museum (Natural History)), London; DORCM – Dorset County Museum, Dorchester, Dorset, England; YPM – Peabody Museum, Yale University, New Haven, Connecticut, USA.


## MULTITUBERCULATE CUSP FORMULAE

Krause (1977) argued that the cusp formulae should reflect the homologies of cusp rows. He stated (Krause 1977, p. 5): 'In most ptilodontoid and taeniolabidoid species there are three rows of cusps on P4; external, middle and internal. The number of cusps in each row is given as a formula x:y:z, where, x, y, and z designate the number of cusps in the external, middle and internal rows respectively. The middle row (y) assuming that it is homologous in all ptilodontoid and taeniolabidoids, is the longest and most cuspidate.' However, Krause did not present evidence to show that the middle (and not for example, internal) row of cusps is homologous in all ptilodontoids and taeniolabidoids. Assuming that the middle row is homologous in all the Cimolodonta, he further argued that the internal row of cusps is absent in several ptilodontoid genera, and the apparently neomorphic 'row' of cusps is often developed labial to the external row (x) of cusps, on an anteroexternal bulge. Consequently he suggested the cusp formula in P4 of *Ptilodus montanus* should not be listed in a traditional way as 0–3:5–8:9–10, but rather as (0–3)5–8:9–10:0. If Krause's proposal were applied to *Albionbaatar denisae*, described below, the cusp formula for P5 should not be written as 5–7:7:7 (as we do), but rather as (5–7)7:7:0, since the buccal row in the P5 of *Albionbaatar* may not be homologous with the buccal row of other plagiaulacoid P5s. We continue to list cusp formulae in all the upper premolars of *Albionbaatar* in the traditional way, as we are of the opinion that with the present limited state of our knowledge on the homology of the cusp rows, it is impossible to demonstrate unequivocally which cusp rows are homologous within the various multituberculate groups. In addition, we are concerned that changes to the terminology may lead to confusion, because the same element would be differently named in new papers.


## STRATIGRAPHY

The teeth described in this paper were extracted from the top 20–40 mm of a clay within the Cherty Freshwater Member of the Purbeck Limestone Formation, about 2·6 m below the base of the Cinder Member. The clay and overlying micritic limestone can be correlated with beds DB 102 and 103 respectively, of the Durlston Bay Purbeck Limestone Formation stratotype (Clements 1969, 1993). West (1988) described both the clay and overlying limestone at Sunnydown Farm Quarry and concluded that they were deposited in environments with 'very low' and 'low' salinities respectively. West suggested that the clays represented extensive mud flats bordering a freshwater lake. The presence of dinosaurs is evident from the considerable number of footprints recorded (Ensom 1987, 1988).

In our earlier discussion (Kielan-Jaworowska and Ensom 1992) of the stratigraphy of the Sunnydown Farm Quarry site and other localities, we pointed out that the Cherty Freshwater Member was currently taken as uppermost Jurassic, with the overlying Cinder Member marking the base of the Cretaceous. This was in line with the published accounts of Rawson *et al.* (1978), following Casey (1963). Consequently, we had described the mammalian fauna as Upper Jurassic (Tithonian), but Lower Cretaceous (Berriasian) may be more appropriate. After our paper was accepted for publication, a review and revision of the correlation of the Purbeck–Wealden in north-west Europe (Allen and Wimbledon 1991) appeared. This highlighted the continuing debate over the position of the Jurassic–Cretaceous boundary in southern England, and the Wessex sub-basin in which these mammal-bearing strata lie was discussed. Allen and Wimbledon pointed out that palynomorph and ostracode evidence would place the Jurassic–Cretaceous boundary more or less at the base of the Purbeck Limestone Formation if the Berriasian *Berriasella jacobi* subzone is ratified as the basal subzone of the Cretaceous. They also noted that use of the marine *Subthurmannia subalpina* subzone as the basal Berriasian subzone would place the Jurassic–Cretaceous boundary at or slightly below the Cinder Member, more or less in line with Casey's proposal. They concluded that an international consensus is required on this matter before the final decision is made. This uncertainty over the age of the material should be born in mind when considering this fauna within the framework of mammalian evolution.

SYSTEMATIC PALAEONTOLOGY

Suborder PLAGIAULACOIDEA (Simpson, 1925) Hahn, 1969
Family ALBIONBAATARIDAE fam. nov.

*Diagnosis.* As for the only known genus *Albionbaatar* gen. nov.

*Stratigraphical and geographical range.* Known only from the Late Jurassic or Early Cretaceous Purbeck Limestone Formation of Southern England.

*Genera.* The family is monotypic.

Genus ALBIONBAATAR gen. nov.

*Derivation of name.* Albion – the oldest, possibly Celtic, name of England, baatar – Mongolian, a hero, a suffix often used for the names of multituberculate genera.

*Diagnosis.* Shrew-sized multituberculate; differs from all multituberculates in having relatively flat, multicusped anterior upper premolars, with ten to fourteen cusps arranged in three rows, rather than three or four, rarely up to nine high cusps in two rows, and in having lingual slope in all premolars covered by prominent, subparallel ridges. Differs from Paulchoffatoidea, known Plagiaulacoidea, Taeniolabidoidea and non-specialized Ptilodontoidea in having P5 with three rows of numerous small cusps. Differs from Paulchoffatoidea in having P5 distinctly longer relative to width. Differs from known Plagiaulacoidea in lack of dramatic difference in the size of the cusps in the same upper premolar. Shares with few derived Cimolodonta (e.g. *Ptilodus*) numerous cusps on posterior upper premolars.

*Albionbaatar denisae* sp. nov.

Plate 1; Plate 2, figures 1–5, 9–10

*Derivation of name.* In honour of Dr Denise Sigogneau-Russell, in recognition of her work on Mesozoic mammals.

*Holotype.* DORCM GS 212 (sample 40) right P5 in a fragment of a maxilla (Pl. 1, figs 3–6; Pl. 2, fig. 10).

*Type horizon and locality.* Cherty Freshwater Member, Purbeck Limestone Formation; near Langton Matravers, Purbeck, Dorset.

*Other material.* DORCM GS 227 (sample 77) right P5; and tentatively assigned: DORCM GS 24 (sample 70) ?right ?P3; DORCM GS 282 (sample 78) ?left ?P2; DORCM GS 23 (sample 95); ?left ?P1, all from the type horizon and locality.

*Diagnosis.* P5 roughly 8 shaped, with buccal and lingual margins incurved in the middle; the holotype specimen is 1·4 mm long, 0·85 mm wide. Cusp formula 5–7:7:7. Buccal row shorter than lingual and median ones, with cusps decreasing in size posteriorly. Cuspules or crenulations present buccal to buccal row.

*Description.* The holotype specimen, right P5 (DORCM GS 212; Pl. 1, figs 3–6; Pl. 2, fig. 10), consists of the crown with two roots, preserved in a small piece of a maxilla. This P5 is roughly 8-shaped in occlusal view, having buccal and lingual margins indented in the middle. It is slightly asymmetrical in this view, as the lingual slope is a little higher (especially posteriorly) than the buccal one. Both anterior and posterior margins are gently rounded, the posterior being somewhat pointed in the middle. The anterior wall is concave in the middle, possibly to receive the posterior part of the crown of the preceding tooth.
    There are seven cusps in the lingual row and the radiating ridges of these cusps continue onto the lingual slope (Pl. 1, figs 3–4; Pl. 2, fig. 10). There are two or three ridges, that start at the tip of each cusp and continue upwards, diverging at the beginning, and then continuing roughly subparallel, some bifurcating in the middle,

all bifurcating on the dorsal part of the slope, the dorsal margin of which is slightly convex and rounded. The lingual ridges of the first three cusps are not abraded and extend upwards and slightly anteriorly along the whole height of the slope. In the midlength of the upper half of the slope, there extends a very weak, longitudinal furrow, about 0·60 mm long and 0·10 mm wide, situated 0·18 mm below the middle part of the dorsal margin of the tooth and 0·33 mm below the posterior part of the margin. The lingual ridges of the fourth and fifth cusps are broken by this furrow and continue upwards above it, reaching the lingual margin, but are less distinct than in the ventral part of the slope. The furrow becomes very shallow posteriorly, extending along the anterior part of the wear facet described below, and disappears 0·26 mm in front of the posterior margin. The lingual ridges of the last two cusps are almost completely worn away. There is a flat wear facet that occupies the posterior quarter of the surface of the lingual slope and reaches the base of the crown. The arrow in Plate 2, figure 10 denotes the direction of poorly preserved wear striations. The height of the lingual slope in the holotype specimen is 0·80 mm anteriorly, 0·66 mm in the middle and 0·83 mm posteriorly.

There are seven cusps in the median row. The buccal and occlusal views appear to show a median row count of eight, as the crenulated anterior margin looks like an additional cusp. The four first are of equal size, the fifth is the smallest, the sixth larger again, the seventh the largest of all. The difference in cusp size is not great. Posteriorly and slightly lingually of the seventh cusp, there is a cuspule with four radiating ridges. The cusps of the buccal row are less regular than those of the lingual and median rows, and vary more strongly in size; defining them as cusps, cuspules or crenulations is sometimes difficult. We recognize five cusps in the anterior half of the tooth, the first of which is lower than the others, ridge-like and elongated longitudinally. The second and third cusps are similar in size and shape to those of the lingual and medial rows, the third being the largest of all in the buccal row. The fourth and fifth cusps are smaller than the third, situated close to each other and joined by a longitudinal ridge running across their tips. To the rear of the fifth cusp, there are irregular crenulations, posterior to which three cuspules extend to the end of the tooth. Buccal to the buccal row there is a single extra cusp, situated opposite the level between the second and the third cusps of the buccal row. To the rear of the extra cusp, the buccal margin, as seen in occlusal view, is developed as an elevated ridge. In buccal view (Pl. 1, fig. 5) this ridge can be seen to be crenulated, which gives an appearance of the presence of the fourth row of cusps, which is not the case. In buccal view, the short vertical ridges extend from this ridge vertically to the buccal margin of the tooth; on the anterobuccal slope in front of the extra cusp, similar ridges are more prominent.

The anterior root, exposed in buccal view, is 1 mm long; only the base of the posterior root is visible (in posterior view).

A right P5 (DORCM GS 227; Pl. 1, figs 7–8; Pl. 2, fig. 9) has been preserved as two fragments that have been glued together. Because of the small size of the tooth, it has proved difficult to reassemble it in its original anatomical position; the posterior region of the tooth should be arranged more horizontally and the posterior end turned more lingually than has been done; after being glued the tooth is possibly longer than it originally was. The bases of both roots are preserved. The tooth is 0·93 mm wide; its length cannot be established, because of the break. It differs from DORCM GS 212 in being less symmetrical, having its anterior margin protruding more strongly in its lingual part than buccally, the posterior margin being less rounded, and the indentations of the buccal and lingual margins situated more anteriorly. The cusps in DORCM GS 227 are insignificantly larger (up to 0·18 mm in diameter rather than up to 0·15 mm in DORCM GS 212). In DORCM GS 227 there are six fully developed cusps in the lingual row and a cusp-like crenulation on the anterior margin giving an appearance of one more cusp. In the median row there are also six fully developed cusps and an anterior cusp-like crenulation of the anterior margin. The important difference with respect to DORCM GS 212 concerns the cusps of the buccal row, which decrease in size posteriorly in both specimens. In DORCM GS 227, there are seven cusps (the third one broken), which up to the end of the row are developed as fully

Figs 1–8. *Albionbaatar denisae* gen. et sp. nov. Cherty Freshwater Member, Purbeck Limestone Formation; Sunnydown Farm Quarry near Langton Matravers, Dorset, England. 1–2, DORCM GS 24; ?right ?P3; occlusal and oblique medio-occlusal views. 3–6, DORCM GS 212, holotype; right P5 with a fragment of a maxilla; occluso-lingual, lingual, buccal and occlusal views. 7–8, DORCM GS 227, plastic cast; broken right P5, glued from two parts; occlusal and buccal views.

All are scanning electron micrographs (all except figure 4 are stereopairs). All teeth are oriented with anterior margin up, and are × 30.

PLATE 1
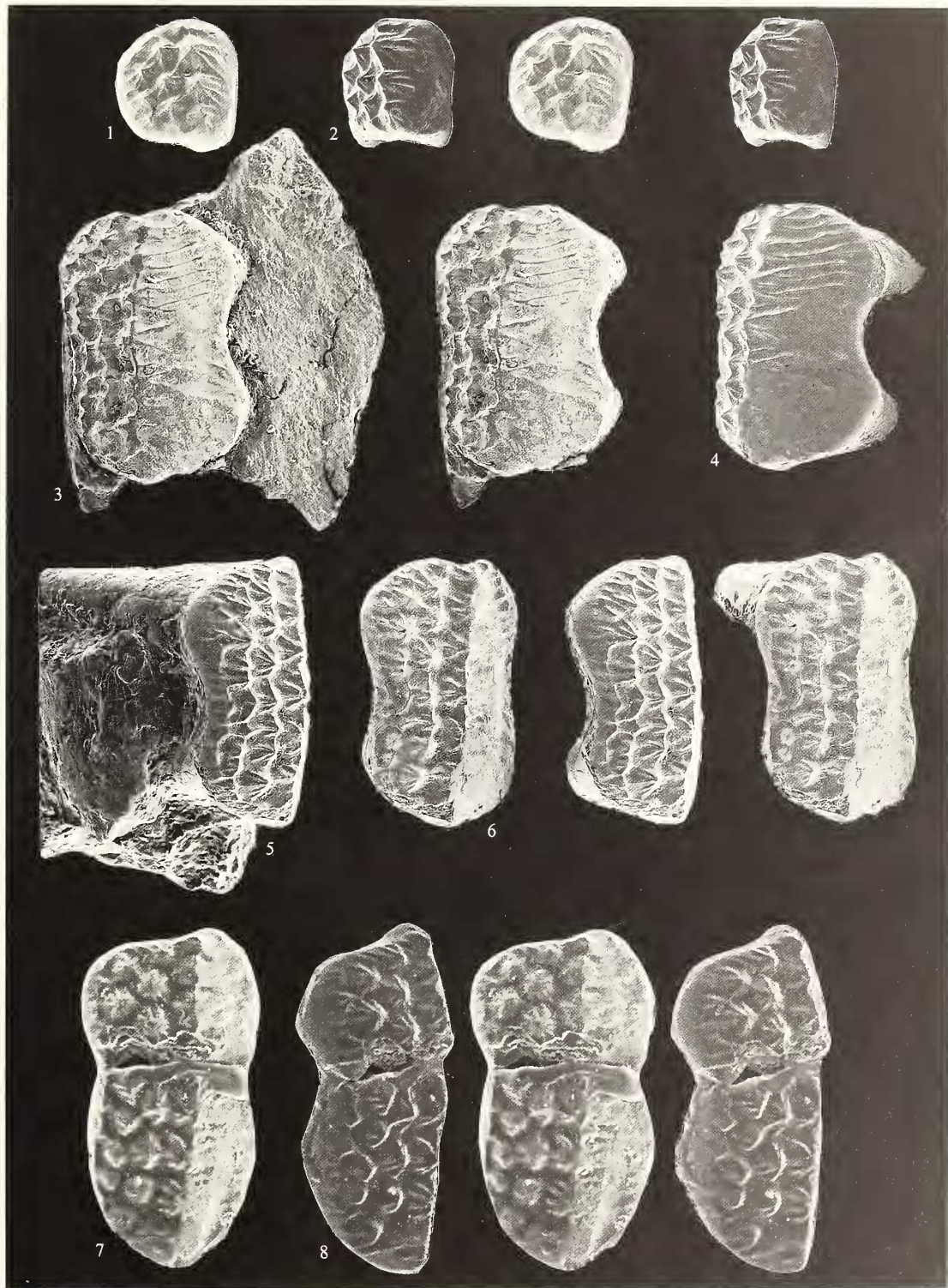
recognizable cusps. In DORCM GS 212 only five fully developed cusps are recognized, and the posterior part of the row is formed by crenulations and cuspules. The single extra cusp present in DORCM GS 212 buccal to the buccal row at the level between the second and third cusps is less obvious in GS 227, resembling rather a crenulation.

The height of the lingual slope in DORCM GS 227 is 0·80 mm above the third cusp, and 0·83 mm above the fifth cusp. The pattern of ridges on the lingual slope differs slightly, but not significantly from DORCM GS 212. The longitudinal furrow extends roughly along the mid-height of the lingual slope and is placed more posteriorly (above the posterior half of the fourth cusp and last three cusps) than in DORCM GS 212. As in the latter the anterior part of the lingual slope is not abraded. The posterior part, opposite the posterior half of the fourth cusp, and the fifth to seventh cusps, is abraded and the degree of wear increases posteriorly. Above the posterior parts of the fourth and fifth cusps and just below the longitudinal furrow, there are small wear facets; the ridges above the furrow are not abraded. Above the sixth cusp there is a large, rectangular wear facet that extends between the tip of the cusp and the longitudinal furrow; only the ridges above the furrow and the first lingual ridge of the sixth cusp are not abraded. Above the seventh cusp the whole area between the tip of the cusp and the longitudinal furrow is completely abraded producing a rectangular wear facet which fits tightly to the longitudinal furrow. Above the furrow the ridges of the seventh cusp are abraded producing a slightly concave wear facet. The seventh cusp is also abraded posteriorly and the crescent-shaped wear facet is present between its tip and the posterior margin of the tooth.

We regard the above cited differences between the two P5s as due to the individual variation within a single species (see Discussion).

A ?left ?P1 (DORCM GS 23; Pl. 2, figs 1–2) is 0·9 mm long lingually, 0·76 mm buccally and 0·73 mm wide, roughly rectangular in occlusal view. The posterior margin protrudes posteriorly in the lingual part. The cusp formula is 3:5:4 with one anterior and three buccal cuspules. The cusps of the lingual slope increase in size posteriorly. The median row has an irregular course; the first three cusps increase in size posteriorly and are arranged longitudinally. The fourth cusp, of approximately the same size as the third, is displaced lingually. The fifth cusp, the smallest, is displaced buccally. There is a small cuspule in front of the buccal row and three cusps in this row which increase in size posteriorly. Buccal to the buccal row there are three cuspules, the first two situated opposite the posterior parts of the first and second cusps, the last one at the posterobuccal corner of the third cusp. All the cuspules are covered with ridges similar to those of the cusps. The lingual slope is covered by the ridges of the lingual cusps, which disappear before reaching the tooth-margin, which is partly broken in this specimen. There are three to four ridges diverging (some bifurcating) from the tip of each cusp up the lingual slope. It cannot be discounted that the tooth is a right one.

A ?left ?P2 (DORCM GS 282; Pl. 2, figs 3–5) is suboval, almost rectangular, wider posteriorly than anteriorly, 0·8 mm long and 0·56 mm wide (measured at one-third of the length from the posterior end). It is possible that the tooth was slightly wider as the buccal margin is partly damaged. The posterior margin is

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EXPLANATION OF PLATE 2

Multituberculates from the Cherty Freshwater Member, Purbeck Limestone Formation; Sunnydown Farm Quarry, near Langton Matravers, Dorset, England.

Figs 1–2. *Albionbaatar denisae* sp. nov. DORCM GS 23; ?left ?P1, roots not preserved; occlusal and dorsal views, 1, × 30; 2, × 20.

Figs 3–5. *Albionbaatar denisae* sp. nov. DORCM GS 282; ?left ?P2; lingual, occluso-lingual and occlusal views; × 30.

Figs 6–7. Plagiaulacoidea, fam., gen. et sp. indet. DORCM GS 22; posterior part of left p4, lingual side broken; buccal and lingual views. 6, × 30; 7, × 20.

Figs 8, 11. Plagiaulacoidea, fam., gen. et sp. indet. DORCM GS 25, plastic cast; anterior part of p4; occlusal and buccal views; × 30.

Fig. 9. *Albionbaatar denisae* sp. nov. DORCM GS 227, plastic cast; right P5; oblique linguo-occlusal view; × 30.

Fig. 10. *Albionbaatar denisae* sp. nov. DORCM GS 212, holotype; right P5; lingual view, only lingual slope shown; arrow denotes the direction of poorly preserved wear striations; × 70.

All are scanning electron micrographs; the specimen in figures 3–5 was not coated with gold; figures 1–8 are stereo-pairs. Upper teeth in figures 1–3 are oriented with anterior margin up, in figures 4–5 and figures 8–9 anterior is to the left.

PLATE 2
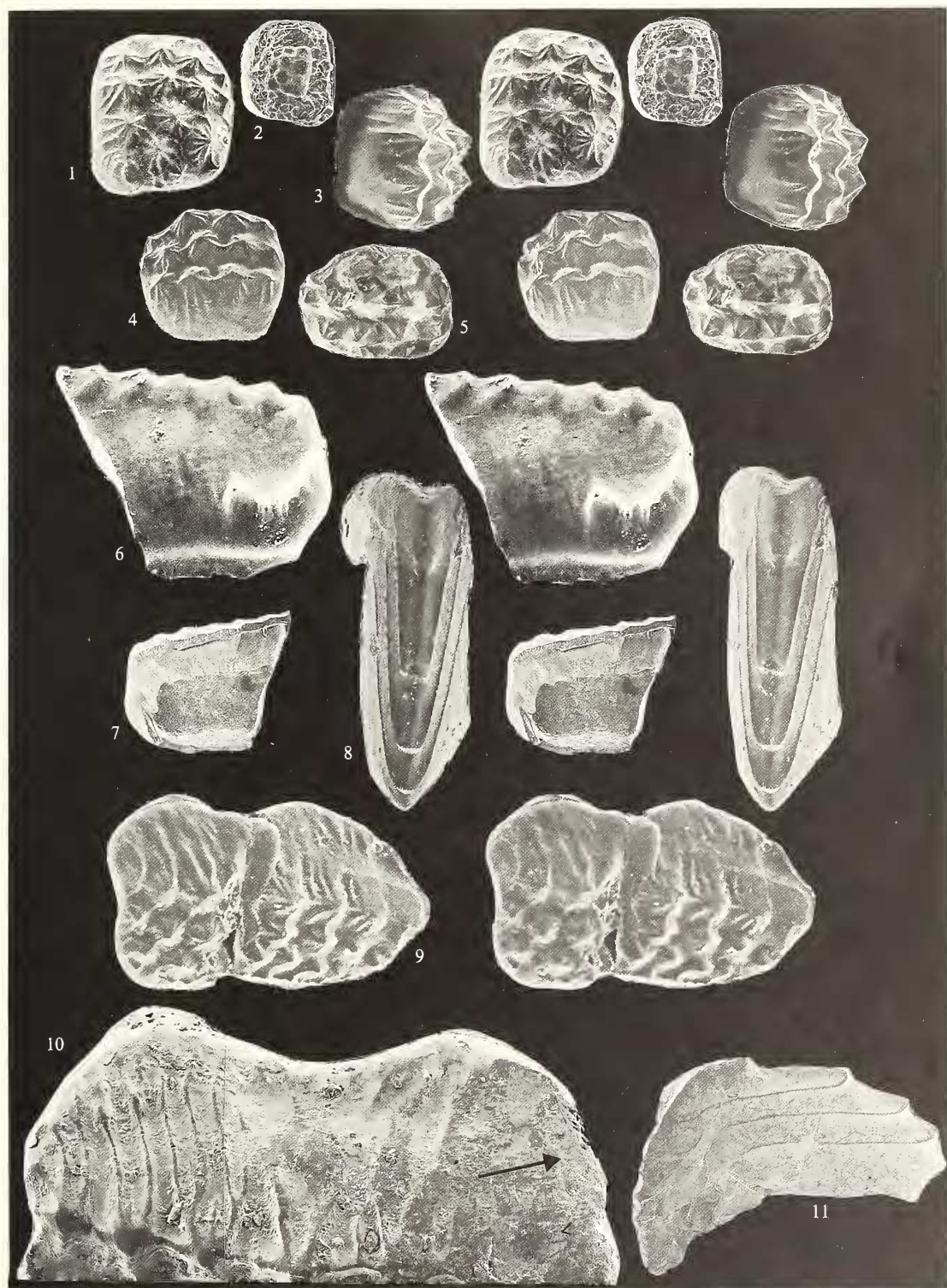


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incurved opposite the buccal row and therefore the tooth is shorter buccally than lingually. The cusp formula is 4:5:4. The anterior cusps in the median and buccal rows (buccal broken) are slightly smaller than the others. The lingual row is relatively high, covered with the ridges of the lingual cusps that extend along its height and disappear before reaching the margin. The posterobuccal part of the slope is smooth, but no wear facet is discernible. It cannot be discounted that the tooth is a right one. It is only slightly shorter than DORCM GS 23, but narrower in respect to the length.

A ?right ?P3 (DORCM GS 24; Pl. 1, figs 1–2) is roughly trapezoid, with the buccal margin shorter than the lingual; 0·7 mm long lingually, 0·5 mm long buccally and 0·6 mm wide. The anterior margin is gently rounded; the posterior margin projects posteriorly opposite the lingual row of cusps. The cusp formula is 4:4:4. The anterior and posterior cusps in the buccal row and the posterior cusp in the median row are smaller than other cusps. The lingual slope is covered with the ridges of the lingual cusps. Two, three or four ridges extend dorsally from each cusp, diverging from the tips; some bifurcate and disappear before reaching the margin of the tooth. The ridges of the two middle cusps are more prominent than the others. The lingual slope is higher than the buccal, especially anteriorly, and is not abraded. It cannot be discounted that the tooth is a left one. It is the smallest tooth of the whole series.

## DISCUSSION

The five teeth assigned to *Albionbaatar denisae* gen. et sp. nov. are identified as upper premolars, because they bear the conical cusps, covered by radiating ridges, characteristic of multituberculate premolars (Krause *et al.* 1992).

We assign the two P5s (DORCM GS 212 and GS 227) to the same species, although they differ slightly in size, as well as in details of the arrangement and size of the cusps, because the amount of variation in size, cusp number, and structure exhibited by these teeth falls within the range of variation seen in larger samples of multituberculates that have been assigned to a single species (see e.g. Clemens 1963*a*; Krause 1977, 1982*b*, 1982*c*, 1987; Rigby 1980; Fox 1980; Johnston and Fox 1984; and many others).

We regard the five upper premolars described above as conspecific, as they display numerous small cusps of the same type arranged in three rows, and similar type of ridges that extend onto the lingual slope. In addition they all roughly fit each other in size.

We identify DORCM GS 212 and DORCM GS 227 as P5s for the following reasons. In plagiaulacoid multituberculates there are five upper premolars. P4 and P5 have been preserved together only in *Bolodon osborni* Simpson, 1928 (BMNH 47735A); *Ctenacodon laticeps* (Marsh, 1881) (YPM 11761); *Psalodon potens* (Marsh, 1887) (YPM 11834), and in the as yet undescribed plagiaulacoid skull from the Morrison Formation, not available to us for this study (Simpson 1928, 1929; Kielan-Jaworowska *et al.* 1987; Engelmann *et al.* 1990; Kielan-Jaworowska and Ensom 1992). In the first three taxa mentioned above there is a continuous extensive lingual wear facet on P4, directed anteroposteriorly and slightly obliquely linguodorsally-buccoventrally. Wear on P5 is more extensive than on P4 and consists of two facets, the anterior one extending for about two-thirds of the tooth length, roughly parallel to the wear facet on P4, and the posterior one arranged obliquely anterolingually-posterobuccally with respect to the sagittal plane (Kielan-Jaworowska and Krause in preparation). The wear pattern of DORCM GS 212 and DORCM GS 227 is different from that on P4 in known Plagiaulacoidea, and is reminiscent of that on P5. However, unlike other plagiaulacoids, in both studied specimens the anterior part of the lingual slope is not worn, and only on the posterior part is a distinct wear facet present. The lack of wear on the anterior part may be due to the young age of the individuals at the time of death. One can presume that in older individuals the wear facet may be developed also on the anterior part of the slope, as characteristic of the Plagiaulacoidea. P5 in the Plagiaulacoidea displays the difference in wear of the anterior and posterior parts of the tooth, while the ultimate upper premolars, P4s in Ptilodontoidea (Krause 1982*a*; see also Wall and Krause 1992) and in eucosmodontid Taeniolabidoidea (personal observations of Z. K.-J.) are worn only in the posterolingual part. The wear striations on the wear facet in both studied P5s are poorly preserved; among the two they are better seen in DORCM GS 212 (Pl. 2, fig. 10) and seem to follow roughly the same (posterodorsal) direction as in P4 of *Ptilodus* (Krause 1982*a*, fig. 9), possibly homologous to P5 in Plagiaulacoidea (Clemens 1963*a*).

Another reason for identifying these teeth as P5s is their elongate shape. The length/width ratio in DORCM GS 212 is 1·64:1, in GS 227 the estimated ratio is about 1·16:1. Known Plagiaulacoidea show the same variation in relative lengths of P4 and P5. In the Allodontidae, both P4 and P5 are relatively short in relation to the width (Simpson 1929; Kielan-Jaworowska et al. 1987). However, in the Plagiaulacidae, e.g. Bolodon osborni, the length/width ratio of P5 is 1·6:1, with an extensive lingual slope, and in P4 the length/width ratio is 1·39:1 with a low lingual slope (Simpson 1928; Kielan-Jaworowska et al. 1987; Kielan-Jaworowska and Ensom 1992). P4 and P5 are unknown in other taxa (Clemens 1963a; Clemens and Lees 1971; Kielan-Jaworowska et al. 1987; Bakker and Carpenter 1990; Engelmann et al. 1990).

In the Cimolodonta (except the specialized Taeniolabididae) P4 (an apparent homologue of P5 in the Plagiaulacoidea, see above) is greatly elongated, although the length/width ratio in various cimolodonts may vary considerably, and the premolars in front of it are all very short. That is why we identify DORCM GS 212 and 227 as P5s rather than P4s. We are confident that DORCM GS 212 and DORCM GS 227 are right teeth, because of the presence of the above mentioned wear facet at only one end (evidently posterior) of the lingual slope.

The identifications of the three anterior upper premolars as P1, P2 or P3 can be only very tentative. Because of the lack of wear facets on these teeth, we were unable to identify them as right or left teeth with any certainty. We therefore put two question marks at each identification, one concerning the side and the other the number of the tooth. We identify DORCM GS 23 as a ?left ?P1, as the cusps on P1 are larger than on successive premolars in a plagiaulacine Bolodon? elongatus. Also, in Bolodon osborni and Ctenacodon laticeps, P1 is larger and has slightly larger cusps than P2 and P3. However, this rule does not always hold, as for example, in Bolodon crassidens, P1 is smaller than P2 and P3 (Simpson 1928, 1929; Kielan-Jaworowska et al. 1987; Kielan-Jaworowska and Ensom 1992). We identify DORCM GS 24 as the ?right ?P3, by comparison with Bolodon osborni, Bolodon? elongatus, Ctenacodon laticeps and Arginbaatar dimitrievae (Kielan-Jaworowska et al. 1987) in which P3 is the smallest of all the upper teeth. We tentatively identify DORCM GS 282 as ?left ?P2, as it is intermediate in size between DORCM GS 23 and DORCM GS 24.

PLAGIAULACOIDEA, fam., gen. et sp. indet.

Plate 2, figures 6–7.

Material. A fragment of the posterior part of the buccal wall of a left p4 (DORCM GS 22, sample 95).

Description. We figure and discuss DORCM GS 22 in this paper, as it was found in the sample yielding DORCM GS 23, identified by us as ?P1 of Albionbaatar denisae. Teeth found in the same sample may belong to the same individual (Kielan-Jaworowska and Ensom 1992).

The preserved fragment of the posterior part of the buccal wall is 1·3 mm long along the dorsal margin and about 1·1 mm high. The preserved fragment shows that the tooth was roughly rectangular and longer than high. The height of the tooth increases anteriorly and the dorsal margin is almost straight. Along the dorsal margin there are seven projections (the seventh incomplete), which are provided with very short anteroventrally directed ridges, more prominent on the two complete anterior projections than posteriorly. The most anterior ridge is 0·2 mm long. The ridge of the last projection is directed more vertically downwards than the anterior ones and widens at the end. In front of the two last ridges there are small rounded depressions, positioned anteroventrally to the serrations between the projections. The posterior margin is vertical in the upper part and bulges posteriorly opposite the posterobuccal cusps, situated in the ventral part of the crown. The posterobuccal cusps are strongly worn from the dorsal side and their joint dorsal margin forms a prominent shelf, concave upwards. Due to the wear it is difficult to estimate how many posterobuccal cusps were originally present; traces of at least five cusps are recognizable. The length of the row of posterobuccal cusps was about 0·6 mm. The preserved part shows that the posterobuccal cusps were prominent, protruding buccally over the surface of the tooth more strongly than in other plagiaulacoid mammals. Along the lower margin of the tooth is a longitudinal furrow. When observed in dorsal view, p4 appears narrower (despite the lingual wall having been broken) than in other multituberculates. Rather than flaring laterally, the buccal wall is arranged almost straight downwards in respect to the narrow dorsal margin, which is indicative of a very narrow tooth. This

is probably the reason why the lingual wall had been broken, a state of preservation rarely found in multituberculate p4s. Another unusual feature of this tooth is that the ventral margin of the buccal wall is bent inwards and the buccal wall possibly overhung the roots, of which there are no traces.

*Remarks.* The roughly rectangular shape of DORCM GS 22 is indicative of the Plagiaulacoidea. The tooth differs from the known plagiaulacoid and other multituberculate p4s in being more knife-like, with buccal and lingual walls placed closer together, rather than flaring outward. In addition, the posterobuccal cusps protrude buccally to a greater extent than in hitherto recorded plagiaulacoids. There are shorter ridges and a ventral horizontal furrow, and the buccal wall of the crown is bent inwards. These two latter features do not occur, as far as we are aware, in known multituberculate taxa. It is impossible to conclude whether DORCM GS 22 is a counterpart of the upper premolars of *Albionbaatar denisae*. Given the structure of the upper premolars of *Albionbaatar* not known to occur in other multituberculates, one can presume, albeit inconclusively, that the p4 in *Albionbaatar* might have a somewhat different structure from those in plagiaulacoid multituberculates, e.g. similar to that in DORCM GS 22.

PLAGIAULACOIDEA, fam. gen. et sp. indet.

Plate 2, figures 8, 11

*Material* DORCM GS 25 (sample 70), anterior part of the left p4.

*Description and comments.* We figure and discuss DORCM GS 25 in this paper, as it was found in the sample yielding DORCM GS 24, identified as ?P3 of *Albionbaatar denisae*.

The size of DORCM GS 25 is difficult to estimate because of its incompleteness. DORCM GS 25 is reminiscent of plagiaulacine genera from Purbeck strata of Great Britain (Simpson 1928; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska and Ensom 1992) in having a gently vaulted dorsal margin, with distinct projections, but it differs from that of *Plagiaulax becklesii* and ?*Plioprion falconeri* in being much smaller, and in having relatively longer ridges that are subhorizontally oriented. It is reminiscent of p4 of *Bolodon osborni* and *B. minor* in having the distance between the first and second projections distinctly longer than between the succeeding ones, but differs from them in having longer ridges which are subhorizontally orientated and in having different lengths between the dorsal projections. In DORCM GS 25 the first projection is situated 0·46 mm to the rear of the anterior margin; the distance between the first and second is 0·5 mm, between the second and third 0·36 mm, and between the third and fourth 0·21 mm. In both species of *Bolodon* the distance between the first and second projections is longer than between the next ones (as in DORCM GS 25), but the distances between the successive ones are of subequal lengths. The anterior wall of DORCM GS 25 (Pl. 2, fig. 8), although damaged, is similar to *B. osborni* in having a triangular dorsal plate and crenulated margins (Kielan-Jaworowska and Nessov 1992, fig. 3A).

DORCM GS 25 is similar to p4s in plagiaulacine taxa. However, given the strong heterodonty between upper and lower premolars in multituberculates, it cannot be ruled out that it might be a counterpart of *Albionbaatar denisae*.

ALLOCATION OF *ALBIONBAATAR* WITHIN MULTITUBERCULATA

*Albaionbaatar* cannot be assigned to the Haramiyoidea (Hahn 1973; Sigogneau-Russell 1989) as all the cusps on the premolars are of equal height and covered by radiating ridges, rather than the cusps being of different heights and lacking ridges. The upper premolars of the Theroteinidae, assigned to Allotheria (Sigogneau-Russell *et al.* 1986; Hahn *et al.* 1989) are not known.

*Albionbaatar* cannot be assigned to the Paulchoffatoidea (Hahn 1969, 1971, 1977; Krause and Hahn 1990), as its fifth upper premolar (P5) is much more elongated in relation to its width than in the Paulchoffatoidea.

Plagiaulacoidea, which are common in the Purbeck Limestone Formation of England (Simpson 1928; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska and Ensom 1992), have an extensive lingual slope in P5 as in *Albionbaatar*, but in contrast to *Albionbaatar*, this slope is not covered by

ridges. The P5 of *Albionbaatar* differs from most (but not all) known members of the Plagiaulacoidea in being more elongated in relation to its width. The most important difference is the presence of three rows of very small and low cusps, which do not differ dramatically in size from each other, rather than one and a half or two rows of relatively large and high cusps, strongly varying in size. Another important difference concerns the number of cusps. In P5 of *Albionbaatar denisae* there are nineteen cusps and six cuspules in DORCM GS 212, and twenty-one cusps and four cuspules in DORCM GS 227. This differs dramatically from the known Plagiaulacoidea, where the number of cusps varies in P5 from six to seven in the Allodontidae, seven cusps and eight cuspules in *Bolodon osborni*, five cusps and seven cuspules in *Bolodon* cf. *minor*, and six cusps in *Eobaatar magnus*. In P4 there are seven cusps in the Allodontidae, seven cusps and four cuspules in *Bolodon osborni*, two cusps and four cuspules in *Bolodon crassidens* and eight cusps and two cuspules in *Eobaatar magnus* (Owen 1854, 1871; Falconer 1857, 1862; Marsh 1887; Simpson 1928, 1929; Kielan-Jaworowska *et al.* 1987; Kielan-Jaworowska and Ensom 1992).

Neither can *Albionbaatar* be assigned to the Cimolodonta (Ptilodontoidea and Taeniolabidoidea) (Granger and Simpson 1929; Simpson 1937; Sloan and Van Valen 1965; Kielan-Jaworowska 1970, 1974; McKenna 1975; Krause 1977, 1982a, 1982b; Clemens and Kielan-Jaworowska 1979; Archibald 1982; Krause and Carlson 1987), as P5 has an extensive lingual slope covered by subparallel ridges, which is not the case in P4 (homologous to P5 of Plagiaulacoidea – Clemens 1963a) of the Cimolodonta. In the taeniolabidid Taeniolabidoidea and in the Cimolomyidae (Granger and Simpson 1929; Clemens 1963a; Sloan and Van Valen 1965; Clemens and Kielan-Jaworowska 1979; Archibald 1982), P4 tends to be reduced and this group does not invite a comparison with *Albionbaatar*. In eucosmodontid taeniolabidoids and in most ptilodontoids (Granger and Simpson 1929; Kielan-Jaworowska 1970, 1974; Clemens and Kielan-Jaworowska 1979) P4 has only one complete (lingual) row of cusps and a short anterobuccal one. However, in some advanced ptilodontoids (e.g. *Ptilodus*), P4 has two more or less complete rows of cusps and a short anterobuccal one, sometimes without cusps. The numbers of cusps in P4s in *Ptilodus* and *Prochetodon* may reach twenty and are thus comparable to those in P5 of *Albionbaatar* (Granger and Simpson 1929; Simpson 1937; Krause 1977, 1982a, 1982b, 1987). However, the ptilodontoid P4 differs dramatically from P5 of *Albionbaatar* in the lack of an extensive lingual slope covered with transverse ridges.

Still more striking differences concern the anterior upper premolars. In *Albionbaatar* these teeth are relatively flat, and bear ten to fourteen small, equal-sized cusps arranged in three rows, whereas in all other multituberculates these teeth bear two to nine high cusps (most often three or four) arranged in two rows.

The upper premolars of the specialized Early Cretaceous Asian Arginbaataridae bear a small number of cusps and differ markedly from those of *Albionbaatar* (Kielan-Jaworowska *et al.* 1987). Another specialized multituberculate family, the South American Ferugliotheriidae (Bonaparte 1986; Krause *et al.* 1992), is known from isolated molars and tentatively assigned anterior upper premolars. These latter teeth do not show a multicusped structure characteristic of *Albionbaatar*.

It follows from the foregoing comparisons that *Albionbaatar*, because of the presence of an extensive lingual slope in P5, is best attributed to the Plagiaulacoidea, although it differs considerably from the known members of this suborder.

Cole and Krause (1988, p. 12A) studied the relationships between tooth size and cusp numbers in Cimolodonta, and concluded: 'These relationships suggest that, at least for taeniolabidoids, tooth size and cusp numbers are not independent and, therefore, that their covariance should be addressed in future studies of multituberculate systematics.' The present study shows that in Plagiaulacoidea as a whole there is no correlation between tooth size and number of cusps, but it seems possible that such a correlation might be found within some plagiaulacoid lines. *Albionbaatar* is amongst the smallest known multituberculates, with minute teeth, which at the same time are characterized by very numerous cusps. Numerous cusps on the upper premolars, but correlated with a large size, were until now known only in advanced representatives of the Cimolodonta.

## CONCLUDING REMARKS

Multituberculates were found in the Purbeck Limestone Formation of England as early as the middle of the nineteenth century (Falconer 1857, 1862). In this paper we have described several minute upper premolars from the rocks of this formation, assigned to the Albionbaataridae fam. nov. within Plagiaulacoidea, and two lower premolars which might be their counterparts.

These teeth have been recovered using the washing and screening technique widely used in vertebrate palaeontology since Hibbard's paper (1949). Palaeontologists searching for Mesozoic mammals often use this technique with sieve meshes down to 1 mm (personal observation). This material has been extracted using a bulk sieving machine constructed to the design of Ward (1981) with sieves of mesh aperture size 0·33 mm. The teeth described here have at least one dimension below 1 mm. Similar teeth may be present in other mammal-bearing strata but previously have been missed.

Because of their superficial similarity with rodents, multituberculates have been sometimes referred to as the rodents of the Mesozoic. Their ecology has been discussed by palaeontologists since the middle of the past century. It has been generally accepted that these were the first mammals that occupied herbivorous niches, although Krause (1982a) demonstrated that they might have been omnivorous. Krause and Jenkins (1983) maintained that some Palaeocene North American multituberculates might have been scansorial in their life-style. Miao (1988) and Kielan-Jaworowska and Qi (1990) suggested fossorial adaptation of Palaeocene-Eocene genus *Lambdopsalis*. Kielan-Jaworowska and Gambaryan are presently describing a collection of the postcranial skeletons of Late Cretaceous multituberculates from the Gobi Desert and showed that multituberculates had abducted limbs. They suggested on the basis of both anatomical and sedimentological evidence, that the life-styles of these multituberculates were similar to those of the modern nocturnal murid rodents (gerbils) that live in semi-desert habitats. However, because of the different limb position, multituberculate locomotion was possibly different from those of small modern rodents, as well as of other small therian mammals which have parasagittal limbs.

The members of the Albionbaataridae belong not only to the smallest multituberculates but possibly to the smallest known mammals as well. As they are known only from a few isolated teeth, the reconstruction of their mode of life poses difficulties.

The Purbeck Limestone Formation is a sequence of limestones, clays and shales of marginal and non-marine origin, at times showing strong terrestrial influence. Within the sequence there is clear evidence of both periods of aridity with evaporite formation, and of freshwater influx permitting the growth of charophytes accompanied by an abundance of freshwater ostracodes and gastropods. Certain horizons within the Cherty Freshwater Member have evidence of both sets of conditions with halite pseudomorphs, charophytes and freshwater invertebrates in close association (Ensom 1985), probably representing seasonal variations of climate. The presence of amphibians in the fauna at Sunnydown Farm Quarry does point to the existence of wetter conditions, in keeping with West's (1988) shallow lake, and certainly more humid than that which existed in the Late Cretaceous of the Gobi Desert.

Multituberculates range in time from the Late Triassic to the Early Oligocene (Hahn and Hahn 1983) and are thus the longest lived order of mammals. It is to be expected that during their long evolutionary history they would adapt themselves to different ecological niches and display an array of life-styles.

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Z. KIELAN-JAWOROWSKA

Paleontologisk Museum
Sars gate 1, Universitctet i Oslo
N-0562 Oslo 5, Norway

P. C. ENSOM

Yorkshire Museum
Museum Gardens
York YO1 2DR, UK